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CONSIDERATIONS OF AGE STRUCTURE IN BACK PROJECTION CALCULATIONS FOR THE NORTHERN OFFSHORE SPOTTED DOLPHIN POPULATION

by

Daniel Goodman

ADMINISTRATIVE REPORT LJ-84-26C

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This report was prepared by Daniel Goodman under Contract Nos. NOAA/83-ABC-0095 and 84-ABA-00873 for the National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California. The statements, findings, conclusions and recommendations herein are those of the author(s) and do not necessarily reflect the views of the National Marine Fisheries Service. Dr. Jay Barlow of the Southwest Fisheries Center served as Chief Official Technical Representative for this contract.

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ABSTRACT

In general, a genuinely age-structured population back-projection, which recovers an unknown past age distribution, starting from a known "present" age distribution, is not feasible. For the case of a spotted dolphin population, we carry out a back-projection to recover the unknown scalar population size of a past population, the age distribution of which is presumed known, starting from a "present" population of known size and unknown age structure.

The above described age-structured back-projection for the dolphin is mathematically well-behaved. It exhibits a sensitivity structure that is essentially the same as that of the back-projection without age structure. The advantage of the age-structured back-calculation procedure, as applied here, is that it makes use of the information concerning age structure of the harvest, which otherwise would be ignored. Owing to the apparent pattern of age selectivity of the harvest, the impact of the harvest as revealed by the age-structured model is somewhat greater than that indicated by an otherwise equivalent non age-structure model. The magnitude of the discrepancy is readily explained in terms of the mean per capita reproductive value of the harvest.

INTRODUCTION

The Management Question

Pursuant to the Marine Mammal Protection Act, it is necessary, in issuing a permit for taking marine mammals, to determine that the target population is above a population threshold called the optimum sustainable population (OSP). Legal and administrative precedent has established that OSP is interpreted as some fraction of the population's numbers prior to the onset of the fishery. The values 0.5 and 0.65 have both been used as the critical fraction for dolphin populations that have been subject to mortality incidental to the eastern Pacific purse-seine tuna fishery.

The purse-seine fleet began taking substantial numbers of

dolphins in 1959. There are no direct estimates of the size of the dolphin populations at that time. There are data bearing on the annual harvests, and there are recent estimates of the population size. Accordingly, the determination of dolphin population status has been accomplished by mathematically back-projecting the population size estimate from the present to 1959, based on estimates of the population's natural mortality and birth rates, and taking into account the estimated numbers harvested. This indirect estimate of the original population size is then compared to the present population estimate to obtain the ratio which, based on its relation to the critical threshold, determines the population's management status.

In past analyses, the back-projection was carried out with a dynamical model that did not incorporate age structure (Smith, 1979). Aspects of the sensitivity of that calculation to uncertainty in the estimates have been discussed elsewhere (Goodman, 1979a; Smith and Polacheck, 1979; Goodman, 1984). The subject of the present paper will be to explore the possible implications of age structured dynamics for the security of the back-projection. Since the question arises in a management context, we shall be primarily concerned with the sensitivity of the decision variable--the estimate of the ratio of present to pre-exploitation population size.

Theoretical Limitations

Age structured population models with overlapping generations are dissipative structures, in that the initial age distribution, with time, becomes irrelevant to the dynamics. This is a negative statement of the more usual description of the positive feature, convergence to stable age distribution. The negative statement is of greater interest to us in this paper, since it results in the original age distribution being unrecoverable by back-projection. Indeed, actual calculation of age structured back-projection will rapidly give rise to impossible numbers. Practical implications of the divergence of age distribution in demographic back-projection are discussed by Greville and Keyfitz (1974); philosophical concerns are discussed by Samuelson (1976).

CONFIGURATION OF THE PROBLEM

Feasible Calculations

We are not, in any case, in a position to attempt an actual age structured back-projection for the dolphin populations, since we do not have firm estimates of the present age distributions of these populations. Only the harvest data are categorized by age.

What we can attempt is an iterative forward projection which converges on a stipulated final (i.e., "present") total population size, from an initial population of unknown size but with a

specified age distribution. A sensible choice for the age distribution of the initial population, since this population is presumed to have been undisturbed, is the stable age distribution associated with the population's life history. This approach really does not tell us anything, other than what we have assumed, about the initial population age distribution, but it does allow us to carry out a back-projection which incorporates information we do have about the age structure of the harvests; and this information will affect the calculated value of the size of the back-projected population.

Interestingly, the age distribution resulting for the final year of the projection is not very sensitive to our assumptions about the initial age distribution. In the absence of the harvest, this would follow immediately from the property of convergence to stable age distribution; under harvest, which may be represented as a time-dependent perturbation in the life table, this follows from the weak ergodicity theorem of Lopez (1961). Indeed, for a sufficiently long projection, the final age distribution is independent of the initial age distribution, and may be calculated directly from the life table and the harvest history (Goodman, 1979b). This determinacy of the final age distribution makes possible a comparison of the computed with the observed age distribution, when such data are available, in a test for internal consistency.

Formally, though it may not be apparent, the projection strategy proposed here has much in common with the suggestion, of Greville and Keyfitz (1974), that a back-projection be carried out by back-projecting the population reproductive value, rather than the population vector itself. Greville and Keyfitz did not consider the situation of a harvest, but a harvest may be incorporated into the type of back-projection they propose by expressing the harvest in units of reproductive value.

Convergence of the Iterative Projection

The iterative forward projection, as described here, involves one unknown, the initial population size, and one criterion quantity, the final population size, which must be acceptably close to the stipulated "known" value. Since the final population size, under the assumption of density independence, is a linear function of the initial population size, iterative correction poses no special difficulties. With density dependence of the vital rates, the relation is no longer linear, but it will still be well-behaved (unless the density dependence is unrealistically intense), allowing for rapid iterative solution.

In fact, for the special case of a time constant life history (corresponding to no density dependence), we may directly obtain an algebraic solution for the back projected population size.

We express the projection algorithm algebraically as

$$\underline{n}_{t+1} = A\,\underline{n}_t - \underline{h}_t \qquad [1]$$

where $\underline{n}_t$ is the population vector at time t, $\underline{h}_t$ is the harvest vector at time t and A is the projection matrix. We see that we can carry out the back-projection as

$$\underline{n}_0 = A^{-t}\,\underline{n}_t + \sum_{j=0}^{t-1} A^{-(j+1)}\,\underline{h}_j \qquad [2]$$

We have specified that the back-projected population vector has a known distribution, which is the stable age vector, $\underline{c}$, calculated from the life table in the usual way (Goodman, 1984), so

$$\underline{n}_0 = s_0\,\underline{c} \qquad [3]$$

where s_0 is the unknown scalar giving the back-projected population size.

We also have specified the scalar value for the final population size, s_t , so

$$s_t = \underline{1} * \underline{n}_t \qquad [4]$$

where $\underline{1}$ is a vector of ones.

Substituting equations [3] into [2] and [2] into [4], and rearranging we obtain

$$s_0 = \frac{s_t + \underline{1}^* \sum_{j=0}^{t-1} A^{(t-j-1)}\,\underline{h}_j}{\underline{1}^*(A^t\,\underline{c})}$$

$$= \lambda^{-t} (s_t + \underline{1}^* \sum_{j=1}^{t-1} A^{(t-j-1)}\,\underline{h}_j) \qquad [5]$$

as the direct solution for the one unknown, s_0 , where λ is the scalar factor of increase (growth rate) associated with the Leslie matrix A.

In general, where density dependence requires iterative solution, a trial value of the initial scalar may be used to project forward, and then the scalar discrepancy between the projected final population size and the stipulated value is simply projected back according to the realized factor of increase associated with the trial projection, and this back-projected scalar is subtracted from the trial value of the initial scalar for the next iteration.

PARAMETERS OF THE PROJECTION

The population we shall consider is the northern offshore spotted dolphin, a form of Stenella attenuata. The history of the harvests, as estimated for the 1979 stock status determination by the National Marine Fisheries Service (Smith,1979), is given in Table 1. The estimate of total numbers in the population, at that time, was 2.76 million--a value which we shall use for the calculations here, though this number is an object of active contention. Recent re-analysis of the same data has concluded that the 1979 population size was between 2.5 and 3.5 million (Holt, 1984).

We shall assume the sex ratio of the 1979 population was 0.5. The sex ratio at birth does not appear to depart from 0.5 (Perrin, Coe and Zweifel, 1976). The sex ratio of the harvest is 0.557 female (Henderson, Perrin and Miller, 1980), which we shall interpret as sex-selectivity of the harvest (consistent with speculation that calves are less adept in escaping from the net, and that their mothers may stay with them). We neglect the slight effect that this posited selective harvest would have on the sex ratio of the 1979 population, since we have no direct data on the matter.

A subsample of the harvest was examined for reproductive status, over the years 1973-1978, and ages were determined from counts of tooth dentinal layers. The aged sample was not really adequate to define the age distribution of the harvest on an annual basis. Furthermore, analysis of the sequence of harvest vectors indicates that the age distribution of the harvest did not change appreciably with time (Barlow and Hohn, 1984). Accordingly, we will treat the age distribution of the harvest as time constant, and estimate it from the pooled sample of aged individuals.

The age classification of the pooled sample, by sex, through the first 16 age classes, is shown in Table 2. The aged subsample was intended to be one half female, by design. Continuing with the assumption that the actual population is one half female, whereas the harvest is 0.557 female, the corresponding estimated fraction of the harvest that are females in the various age classes is given in Table 3.

The age notation we shall use here refers to the youngest age class, individuals from birth to their first birthday, as class 1. We shall define the life history parameters according to the discrete time convention described in Goodman (1982), assuming seasonal reproduction, and census just before the calving season.

There are no firm data bearing directly on natural mortality rates for the dolphins. Barlow (1984) has derived an estimated mortality schedule for the dolphin on the basis of the oldest observed ages in the subsample of the harvest, and by comparative calibration of mammal mortality schedules in terms of the age at which survivorship is reduced to 5%. The model survival rate schedule, expressed in terms of our age notation (but not Barlow's), for a life history where the age at 5% survivorship is 40, is shown in Table 4. We shall use this probably optimistic survival rate schedule to represent the dolphin life table.

On the basis of the reproductive status of the females in the aged subsamples, the fraction mature, at each age, and the reproductive rates of mature females in various age categories have been estimated (Myrick, Hohn, Barlow and Sloan, 1983). The approach to maturity with age, in the 1973-1978 subsample, was fit with a logistic curve, where the age notation treated individuals from birth to first birthday as age class 0, etc., (Myrick et al., 1983, fig 5). To convert to mean fraction mature for age classes centered on the birthday in our age notation, we interpolate to their half year positions and subtract 0.5 from their nominal age. For ages 9 and younger, we use the value zero rather than the interpolated logistic, because the aged subsample contained no mature animals younger than 10. The resulting model maturity ogive is shown in Table 4.

Examination of evidence of numbers of prior pregnancies in the aged subsample of females, indicates that the reproductive cycle for mature females is 3 years (Myrick et al., 1983), consistent with the estimates, on other grounds (Perrin et al., 1976), that the gestation period is almost 1 year, that the obligate nursing period is about one year, and that there is a third year of close association between calf and mother, with occasional nursing, before the next birth. The brood size is invariably one.

Using 3 years as the the interbrood interval, taking the sex ratio at birth to be 0.5, incorporating Barlow's (1984) value of 0.85 as the intrinsic survival rate of newborn from birth until the time of first "census" corresponding to our age class 1, and further incorporating the age specific survival rate of females to account for the probability of calf mortality owing to loss of the parent before the first census, we obtain from the maturity schedule of Table 4 the discrete time effective fecundity schedule shown in Table 5. We neglect additional calf mortality, owing to loss of the parent in the

second and third years of life.

The model survival rate schedule of Table 4 and the model fecundity schedule of Table 5 result in an asymptotic factor of population increase (discrete time population growth rate) of 1.0298, roughly 3% per annum. The associated survivorship schedule, stable age distribution, and age specific reproductive values are also shown in Table 5.

This model life history contains a bit too much detail for our purposes here, since the age determinations of the older individuals in the harvest are not secure, the sample size of older animals that were aged is small, and in any case the details of the mortality schedule are speculative. Accordingly, we condense this life history in a geometric series parametrization (Goodman, 1984), using 11 as the age at maturity. This yields a mean per capita adult survival rate of 0.956, a mean per capita adult fecundity rate of 0.125, and a survivorship to adult status of 0.786. The population growth rate under this parametrization is mathematically identical to that of the full life history, as are the survivorships and stable age distribution of all age classes younger than the age at nominal maturity, and the age specific reproductive values of all genuinely pre-reproductive age classes. The parametrization is not innoccuous, however, for it does affect the reproductive value of the "mature" class.

The consensus during the 1979 status determination, when the age of maturity was thought to be considerably younger than the current estimate, was that the natural mortality rate of adults must lie between 0.05 and 0.15 per year, expressed on a discrete time basis. The new model yields an adult mortality rate just beyond the lower limit of that range, and a mortality from birth to reproductive age that is considerably less than assuming a constant 5% mortality over age classes 1 through 10. Because critical data on mortality rates are not available, we are not in a position to comment further on the probability that the life history model developed above is an accurate representation for the northern offshore spotted dolphin. We will proceed with the geometric series model to illustrate the possibility of effects of age structure on the back-projection, but without arguing that the resultant back-projection yields a value that is correct for this population.

Even with quite generous assumptions about natural mortality, the parameter that is least constrained by the data, the resulting factor of increase, is very near simple replacement. Therefore, the incorporation of density dependence in the model would make little difference, and since, in any case, we have no data bearing on the form of density dependence for this population, we will omit density dependence from the present analysis. Since the life history we use throughout the projection is that which is thought to apply to the recent populations, which would have the highest growth rate under a density compensation model, our decision to ignore density dependence is also generous with respect to predictions about the ability of the population to withstand harvest.

RESULTS AND DISCUSSION

Age Structured Back-projection

The parameters defined above result in a back-projection to a population size of 2.77 million females in 1959, yielding 0.497 for the ratio of "present" to pre-exploitation population size, as of 1979 (i.e., N1979/N1959). The age distribution of the final population is shown in Table 6, with the stable age distribution for comparison.

Obviously, the resulting age distribution departs so little from the stable age distribution, that, in this case, analysis of the age distribution of the present population will not be revealing, except as a test of internal consistency on the assumed natural mortality rate. The system does not have sufficient contrast to use the distortion of the age distribution for an independent estimate of the population size.

It is noteworthy, nevertheless, that the resulting age distribution shows no deficit in the mature age classes, even though the harvest selectively removes mature individuals, as may be seen by comparing the age distribution of harvest with the stable age distribution under the life history parametrization, shown in Table 7. This discrepancy is accounted for by the declining trend in the total harvests over the past decade (Table 1). Essentially, the harvest has been relaxed for a period of time that is just insufficient for the resulting stronger year classes to reach maturity.

Table 8 shows the resulting final age distribution for a simulation where the same total harvest, of 4.427 million individuals is evenly distributed over the twenty year interval, rather than following the sequence of Table 1. Here, as expected, the slightly selective harvest does result in a deficit in the mature age classes, relative to the stable age distribution.

Back-projection Without Age Structure

If we ignore age structure, and simply back-project total female numbers according to the factor of increase and the annual harvest, the calculated initial female population size is 2.71 million, for a ratio of present to pre-exploitation population size of 0.509, which is a larger value (by about 2.4%) than indicated by the age-structured model. Thus, the back-projection without age structure presents a slightly more optimistic view of the population status.

The primary source of the discrepancy lies in the slight selectivity of the harvest. Refering to Table 7, we see that the immature age classes are all somewhat underrepresented in the

harvest, relative to the reproductive class. The reproductive class, of course, has the higher reproductive value per individual (Table 7). As a consequence, the mean reproductive value, per individual, in the harvest is 1.566 compared to 1.517 in the stable age distribution--roughly a 3.3% difference.

In other words, the age selectivity of the harvest results in a somewhat greater impact on the population than is revealed simply by a count of the numbers taken. Further, since the remaining population generally has a perturbed age distribution with a deficit of reproductive animals, the realized growth rate of this population will be less than the natural life history's factor of increase, thus compounding the error if the factor of increase is simply used to back-project total numbers.

Sensitivity of the Back-projection

Inspection of equation [5] gives some impression of the roles of the harvest, the final population estimate, and the life history, in determining the back-projected population size. Under the conditions of this back-projection, the process of reconstituting the past population size, s_0 , is accomplished simply by correcting the final population s_t for the sequence of harvests, and then back-projecting the result according to the scalar factor of increase, λ , of the underlying life history. We see immediately that the driving variables in the back-projection are s_t , λ and the magnitude of the harvests.

The details of the life table, except as they affect the value of λ , only enter into the term in the summation, where the Leslie matrix is applied to the age structured harvests. For harvests suffered long before the final time horizon (i.e., for early harvests), the term $A^{(t-j-1)}$ behaves essentially as $\lambda^{(t-j-1)}$ times the dot product of the harvest vector and the scaled schedule of reproductive values. In other words, the major role of the details of the life table, beyond the magnitude of growth rate, is in the effect of the age distribution of the harvest, mediated primarily by the total reproductive value of the harvest.

The roles of the population estimate and the factor of increase, in the non age-structured analysis have been explored previously (Goodman, 1979a; Smith and Polacheck, 1979), and the relationship of vital rates to the factor of increase has been treated in some detail (Goodman, 1984). It seems unlikely, in principle, that an age-structured projection should differ appreciably in its sensitivity structure, and indeed we find it much the same.

In Table 9, first derivatives, calculated as finite differences, of the factor of increase and of the decision ratio,

with and without age structure, are shown with respect to variation in the factor of increase, the survival rate, the effective fecundity, the estimate of the final (1979) female population, the total harvest, and an aspect of the age composition of the harvest.

Varying the factor of increase alone, without adjusting the component vital rates, is not compatible with an age-structured model, so this result pertains only to the model without age structure. The resulting derivative for N1979/N1959 will be helpful in understanding how much of the sensitivity to variation in components of the life history is mediated essentially by an effect on the factor of increase.

Varying the survival rate results in adjustments to the effective fecundity and the immature survival rates, owing to the incorporation of the fundamental survival rate term in their estimation, as explained in Section III. The resulting effect on the factor of increase is about the same as the effect of varying the factor of increase directly, and the result for the decision ratio is likewise about the same as the effect of varying the factor of increase directly, indicating that the effect is mediated essentially through the factor of increase. The results for the age-structured and non age-structured back-projections are very similar.

Varying the effective fecundity alone, results in about 1/4 the effect on the factor of increase as varying the factor of increase directly, and the result for the decision ratio is likewise about 1/4 the effect of varying the factor of increase directly, indicating that the effect is mediated essentially through the factor of increase. The results for the age-structured and non age-structured back projections are similar.

Varying the estimate of the final population size has no influence on the factor of increase; it does affect the age-structured and the non age-structured back projections in a modest, and very similar, way.

Varying the estimate of the total harvest was computed with respect to summed harvests, over all ages, over all years, over both sexes, with the constraint that the sex ratio, age distribution, and tne proportion of the harvest accounted for by each year remain fixed. Varying the total harvest, of course, has no influence on the factor of increase, and it leads to small, and very similar, effects in the age-structured and non age-structured back projections.

Varying the estimate of the fraction of the harvest that are females in age class 1 was accomplished by trading this fraction against the fraction in the mature class, keeping the sex ratio and total size of the harvest constant. Obviously, this has no effect on the factor of increase or the non age-structured back-projection, but it does substantially affect the result of the age-structured back-projection.

Expressing the sensitivities in terms of a fractional perturbation, rather than a unit change, facilitates comparison between factors. This is accomplished by multiplying the derivative with respect to each variable by the magnitude of that variable. As a further convenience, if we then rescale, dividing by the magnitude of the variable whose derivative we are considering, we will have achieved a normalization that converts a fractional perturbation in the "input" variable (e.g., total harvest, adult survival rate, etc.) to a resulting fractional effect on the "output" variable (e.g., N1979/N1959). This scaling is shown in Table 10, where we see that the back-projection is more sensitive to variation in the factor of increase than to variation in the harvest or the population estimate; and, as is by now common knowledge, the mortality rate, for life tables of this sort, is the most critical variable in determining the factor of increase. The sensitivities to the final population estimate and the total harvest are nearly identical. Effects of age structure of the harvest can only be revealed in an age-structured model, where the sensitivity to variation in the youngest age class (which comprise a very small fraction of the harvest) is comparatively small, though the sensitivity to variation in fraction of the mature age classes in the harvest is appreciable, but still less than the sensitivity to the dynamical or census parameters.

Even though the sensitivities of back-projections with and without age structure are very similar, the non age-structured model consistently displays slightly greater derivatives with respect to the same variable. This is in part due to the artificiality of scaling the decision criterion simply as the total number of individuals in the age structured model. Age-structured population dynamics of long-lived organisms are somewhat buffered against perturbations in total numbers owing to the overlap of generations. If the decision criterion were expressed in units of total reproductive value rather than total numbers, a slightly greater variability would appear.

CONCLUSIONS

There is no prospect of literally carrying out an age-structured back-projection calculation for the harvested dolphin populations in order to reconstruct the past age distribution from present information. An age-structured back-projection, assuming that the pre-exploitation population was in stable age distribution, can be carried out to estimate the total pre-exploitation population size with somewhat greater accuracy than is achieved by a non age-structured back-projection, since this makes use of the age structure information about the harvest.

Since the aged subsamples of the harvest indicate that the harvest was selectively removing mature individuals, the actual impact of this harvest is greater than was revealed in a non age-structured back projection. In the present example, the

age-structured back-projection showed a slightly smaller value for the ratio N1979/N1959 than did the back-projection based simply on total numbers. The discrepancy was about 2.4%. We noted that the age selectivity of the harvest resulted in the mean per capita reproductive value of the harvest being about 3.3% greater than the mean per capita reproductive value of a population in stable age distribution: this is equivalent to saying that the simple tally of numbers harvested underestimates the the effect of the numbers harvested as if the total numbers harvested, in a non age-structured back-projection, were itself underestimated by 3.3%. Applying the proportional sensitivity of the non age-structured model with respect to the total harvest (-0.717 from Table 10) to the 3.3% underestimate of total harvest, predicts a 2.4% overestimate of N1979/N1959, substantially accounting for the observed discrepancy.

Sensitivity analysis of the age-structured back-projection turned up no surprises. Except for the effects of age structure of the harvest, which are of course supressed in the non age-structured model, the sensitivities of the age-structured model to variations in model parameters are very similar to those of the non age-structured model. The sensitivity to the dynamical parameter, population growth rate, is appreciably greater than the sensitivity to census information or total harvest; and the natural mortality rate is the most crucial element in determining the dynamics. The sensitivity to age structure of the harvest is very small for the youngest age classes, but for the mature class it approaches the order of the sensitivity to census information, and it is substantially less important than the sensitivity to the population growth rate.

We conclude that there can be an appreciable effect of age structure of a harvest in computing a back-projected estimate of pre-exploitation population size, and that the effect is readily incorporated into an appropriate model. The magnitude of the effect will increase with the discrepancy between the mean per capita reproductive value of harvests and the mean per capita reproductive value in the stable age distribution. The back-projection model will be well-behaved provided it is structured to recover the scalar magnitude of the past population size, without attempting to recover the past age distribution.

The illustrated calculation of the effects for a back-projection of the northern offshore spotted dolphin exhibit these features. The reality of the actual values computed in this back-projection is uncertain, owing primarily to the uncertainty regarding natural mortality rates. There is a further unfortunate ambiguity in that the aged subsamples of the harvest do not include the period of most massive harvests, and do include a period when there was a declining trend in the harvest with associated transients in the population age distribution, so we are not assured that the age distribution data which we have for the harvest are truly representative for the bulk of the history of the fishery. Finally, there is a suspicion that the neonates, which comprise a bit less

than half of the youngest age class in the model, were somewhat underrepresented in the aged subsample (A. A. Hohn, pers. com. 1984).

ACKNOWLEDGEMENTS

Jay Barlow made many important suggestions in the development of this analysis. Aleta Hohn was of great help in explaining the life history and aging data. The research was supported by NOAA contracts 83-ABC-0095 and 84-ABA-00873.

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Table 1. Estimated total incidental kill of northern offshore spotted dolphin, by year.

(1959)	82539
(1960)	409908
(1961)	460063
(1962)	189485
(1963)	204382
(1964)	332646
(1965)	361061
(1966)	324197
(1967)	216252
(1968)	187628
(1969)	382843
(1970)	371328
(1971)	184326
(1972)	298154
(1973)	131863
(1974)	95643
(1975)	105564
(1976)	47460
(1977)	22549
(1978)	19241

Table 2. Frequencies of individuals per age class in the pooled aged subsamples of the kill from the years 1973-1978. The sex ratio of the subsample is about 0.5 by design.

	female	male
(1)	34	47
(2)	40	47
(3)	38	36
(4)	39	52
(5)	24	27
(6)	15	36
(7)	17	28
(8)	9	26
(9)	23	21
(10)	19	30
(11)	23	25
(12)	34	32
(13)	26	18
(14)	24	17
(15)	21	32
(16+)	391	323

Table 3. Estimated fraction of the total harvest that are females in the respective age classes. The total harvest is 0.577 female.

age class	fraction of kill
(1)	0.0244
(2)	0.0287
(3)	0.0272
(4)	0.0280
(5)	0.0172
(6)	0.0108
(7)	0.0122
(8)	0.0065
(9)	0.0165
(10)	0.0136
(11+)	0.3721

Table 4. Model schedule of survival rate, adapted from Barlow (1984), and fraction mature, adated from Myrick, et al. (1984), according to a discrete time notation where the youngest age class is 1 and the census is just prior to calving.

age class	survival rate	fraction mature
(1)	0.900	0.00
(2)	0.985	0.00
(3)	0.985	0.00
(4)	0.985	0.00
(5)	0.985	0.00
(6)	0.985	0.00
(7)	0.985	0.00
(8)	0.985	0.00
(9)	0.985	0.00
(10)	0.985	0.27
(11)	0.985	0.44
(12)	0.985	0.62
(13)	0.983	0.78
(14)	0.982	0.90
(15)	0.980	0.95
(16)	0.979	0.98
(17)	0.977	0.99
(18)	0.975	1.00
(19)	0.973	1.00
(20)	0.970	1.00
(21)	0.967	1.00
(22)	0.964	1.00
(23)	0.960	1.00
(24)	0.955	1.00
(25)	0.950	1.00
(26)	0.944	1.00
(27)	0.937	1.00
(28)	0.929	1.00
(29)	0.920	1.00
(30)	0.910	1.00
(31)	0.989	1.00
(32)	0.885	1.00
(33)	0.870	1.00
(34)	0.853	1.00
(35)	0.834	1.00
(36)	0.813	1.00
(37)	0.789	1.00
(38)	0.763	1.00
(39)	0.734	1.00
(40)	0.702	1.00
(41)	0.667	1.00
(42)	0.632	1.00
(43)	0.590	1.00
(44)	0.000	1.00

Table 5. Schedules of survivorship, fecundity, stable age distribution and age specific reproductive value in the model dolphin life history.

age class	survivorship	fecundity	stable age distribution	reproductive value
(1)	1.000	0.000	0.063	1.000
(2)	0.900	0.000	0.055	1.144
(3)	0.887	0.000	0.053	1.196
(4)	0.873	0.000	0.051	1.251
(5)	0.860	0.000	0.048	1.308
(6)	0.847	0.000	0.046	1.367
(7)	0.834	0.000	0.044	1.430
(8)	0.822	0.000	0.042	1.495
(9)	0.810	0.000	0.040	1.563
(10)	0.798	0.038	0.039	1.634
(11)	0.786	0.061	0.037	1.670
(12)	0.774	0.087	0.035	1.684
(13)	0.762	0.109	0.034	1.672
(14)	0.749	0.125	0.032	1.642
(15)	0.736	0.132	0.031	1.594
(16)	0.721	0.136	0.029	1.541
(17)	0.706	0.137	0.028	1.482
(18)	0.690	0.138	0.026	1.422
(19)	0.672	0.138	0.025	1.360
(20)	0.654	0.137	0.024	1.298
(21)	0.635	0.137	0.022	1.236
(22)	0.614	0.137	0.021	1.175
(23)	0.592	0.136	0.020	1.113
(24)	0.568	0.135	0.018	1.053
(25)	0.542	0.135	0.017	0.993
(26)	0.515	0.134	0.016	0.935
(27)	0.486	0.133	0.014	0.879
(28)	0.456	0.132	0.013	0.824
(29)	0.423	0.130	0.012	0.772
(30)	0.390	0.129	0.010	0.722
(31)	0.354	0.140	0.009	0.676
(32)	0.351	0.125	0.009	0.562
(33)	0.310	0.123	0.008	0.512
(34)	0.270	0.121	0.006	0.465
(35)	0.230	0.118	0.005	0.420
(36)	0.192	0.115	0.004	0.376
(37)	0.156	0.112	0.003	0.335
(38)	0.123	0.108	0.003	0.296
(39)	0.094	0.104	0.002	0.257
(40)	0.069	0.099	0.001	0.219
(41)	0.048	0.094	0.001	0.180
(42)	0.032	0.090	0.001	0.137
(43)	0.020	0.084	0.000	0.081
(44)	0.012	0.000	0.000	0.000

Table 6. Age distribution of the modeled 1979 female population, compared to the stable age distribution associated with the undisturbed life history.

	population age distribution	stable age distribution
(1)	.063	.063
(2)	.055	.055
(3)	.052	.053
(4)	.049	.051
(5)	.046	.048
(6)	.044	.046
(7)	.044	.044
(8)	.042	.042
(9)	.043	.040
(10)	.042	.039
(11+)	.519	.518

Table 7. Age composition of the female segment of the kill, compared with the stable age distribution of the unharvested life history, and the vector of reproductive value associated with that life history. The assumed life history parameters are given in the text.

	kill age distribution	stable age distribution	reproductive value
(1)	.044	.063	1.00
(2)	.051	.055	1.14
(3)	.049	.053	1.20
(4)	.050	.051	1.25
(5)	.031	.048	1.31
(6)	.019	.046	1.37
(7)	.022	.044	1.43
(8)	.012	.042	1.49
(9)	.030	.040	1.56
(10)	.024	.039	1.63
(11+)	.668	.518	1.71

Table 8. Age distribution of the modeled 1979 female population after projection with a time constant harvest corresponding to the mean harvest in the 1959-1978 period, with the stable age distribution for comparison.

	population age distribution	stable age distribution
(1)	.061	.063
(2)	.054	.055
(3)	.052	.053
(4)	.050	.051
(5)	.050	.048
(6)	.050	.046
(7)	.050	.044
(8)	.051	.042
(9)	.050	.040
(10)	.049	.039
(11+)	.484	.518

Table 9. First derivatives of back-projection parameters and results, with respect to various input parameters:

Parameter	Derivative of--		
	Factor of increase	Age-structured N1979/N1959	Non age-structured N1979/N1959
factor of increase	1.000	------	5.734
survival rate	1.167	6.263	6.511
effective fecundity	0.342	1.593	1.901
final population in millions	0.000	0.261	0.265
total harvest in millions	0.000	-0.081	-0.082
fraction of age class 1 in harvest	0.000	0.287	0.000

Table 10. Sensitivities of back-projection parameters, and back-projection results, to various input parameters, expressed as the sensitivity to a proportional change in the input parameter, computed as the first derivative with respect to the input parameter multiplied by the magnitude of that input parameter:

Parameter	Sensitivity of--		
	Factor of increase	Age-structured N1979/N1959	Non age-structured N1979/N1959
factor of increase	1.000	------	11.306
survival rate	1.086	12.066	12.252
effective fecundity	0.042	0.403	0.470
final population	0.000	0.725	0.718
total harvest	0.000	-0.724	-0.717
fraction of age class 1 in harvest	0.000	0.014	0.000
fraction of age class 11+ in harvest	0.000	-.215	0.000